SOIL FAUNA AND SOIL STRUCTURE: FEEDBACK BETWEEN SIZE AND ARCHITECTURE

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ABSTRACT

The relations between soil fauna and soil structure are examined using papers from this conference as a background. Our synthesis focuses on function of the soil system and reciprocity between soil animals and other soil components.

Advancement of knowledge at this interface has been impeded by disciplinary specialization and isolation, and failure to frame hypotheses and research strategies in the context of the entire soil system. Two major challenges must be met before progress will be possible. First, philosophical beliefs about soil must be separated from objective science. The second problem is mainly taxonomic. For soil animals, problems of correlating phylogenetic and ecological groupings must be resolved. For soil micromorphology, classifications must be simplified and made more accessible to soil ecologists.

We conclude that soil animals regulate soil function through both trophic interactions and biophysical mechanisms which influence microhabitat architecture. The mixed culture aspect of soil communities involves diverse species interactions which regulate the structure of soil communities. We propose that comminution and disintegration of microstructures be added to formation of microstructures and comminution of plant debris as a third biophysical regulatory mechanism. This leads to a dynamic view of micropedology. Establishing links between groups of soil organisms and specific soil microstructures as seen in thin section will require substantial collaborative effort. Such efforts will yield basic information necessary for solving pressing applied problems in management of renewable resources depending upon soil.

RÉSUMÉ

Nous synthétisons les rapports entre la faune édaphique et la structure des sols à la lumière des articles présentés au cours de la conférence. Cette synthèse se concentre sur les fonctions des sols en tant que systèmes et sur la réciprocité des rapports entre les animaux édaphiques et les autres composantes du sol.

Le progrès des connaissances à ce niveau a été entravé par la spécialisation et l'isolement des diverses disciplines, et par le manquement à formuler des hypothèses et des stratégies de recherche qui considèrent les systèmes édaphiques dans leur ensemble. Deux défis de taille doivent être confrontés si l'on est pour progresser. D'abord il faut séparer les convictions philosophiques au sujet du sol de l'approche scientifique objective. Deuxièmement, il faut surmonter les problèmes taxonomiques. En ce qui concerne la faune édaphique, il faut réussir à corréler les groupes phylogénétiques avec les groupes écologiques. En ce qui concerne la micromorphologie des sols, il est nécessaire de simplifier les *classifications et de les rendre plus accessibles aux écologistes étudiant les sols.*

Nous concluons que les animaux édaphiques régularisent la fonction du sol par des interactions entre les niveaux trophiques et par des mécanismes biophysiques qui affectent l'architecture des microhabitats. L'apparence de culture mélangée que présentent les communités édaphiques met en jeu des interactions diverses entre les espèces qui régularisent la structure de ces communautés. Nous proposons que la pulvérisation des débris et la désintégration des microstructures soient considérées comme formant un troisième mécanisme régulatoire biophysique en plus de ceux de la formation des microstructures et de la pulvérisation des débris végétaux. De cette façon on obtient une image dynamique de la micropédologie. L'établissement de liens entre les groupes d'organismes édaphiques et les microstructures spécifiques des sols requièrera des efforts de collaboration substantiels. De tels efforts permettront d'obtenir des informations fondamentales nécessaires pour résoudre les problèmes pratiques d'aménagement des ressources renouvelables qui dépendent du sol.

INTRODUCTION

As the circle of knowledge increases, so too does the fringe of ignorance. An objective of this conference was to increase knowledge without expanding the fringe of ignorance by combining results of analyses from two spheres: soil micromorphology and soil zoology. The mathematical proof of the above possibility is simple, but the challenge of bringing about constructive interaction between soil micromorphologists and soil zoologists is not.

Since the pioneering work of Kubiena (1938) we have known that soil structure and function are intimately related. In this conference, papers by Hill and Parkinson showed that soil animals regulate other soil biota both directly and by altering their environment. Altemüller, Mermut, Pawluk and Rusek showed convincingly that soil animals play a large role in organizing and maintaining soil fabrics.

Increased understanding of relations between soil fauna and soil structure will have important practical benefits. For example, Hill remarked that sustained agriculture depends on understanding the regulation of complex biological processes occurring in soil rather than indiscriminately accelerating a few. Several authors repeated the theme that soil animals contribute to soil quality and modify soil profiles and nutrient supply to agricultural crops. In particular, the paper by Edwards summarizes information now available about the importance of earthworms, a topic that was first studied experimentally by Charles Darwin (1881). Papers by Greenslade, Mermut, Pawluk and Rusek showed that animals generate structural units in soils from the Arctic through temperate regions to the tropics.

Despite immense opportunities for both basic and applied research, soil ecology has remained a relatively unstudied discipline. The generality of much ecological theory, developed from studies of freshwater and terrestrial systems, could be tested by work with soil systems. Also, working out the relationships among biotic and abiotic components of the soil can provide interesting proximate frameworks for research. Mechanistic questions about relationships between soil fauna and soil structure have been raised by most speakers. For example, both Dindal and Norton pointed out the apparent paradox of persistence of faecal pellets associated with increased rates of decomposition in the presence of soil animals. An important question, raised by Foster's presentation, is the extent to which soil animals are involved in disintegration of fundamental soil structural units. Resolution of such questions will increase understanding of the important but poorly understood decomposer food web.

In this paper we review some of the past impediments to interaction between soil zoologists and soil micromorphologists, develop the concept of the soil system as the unifying link between their disciplines, and present some ideas flowing from such a conceptual approach to studying relationships among soil animals and soil structure.

IMPEDIMENTS

In North America, soil morphologists and soil zoologists have not communicated in the recent past, in part due to a tradition of geological affinity of the former group and the predominant zoological background of those interested in soil animals. For both groups, the focus of attention frequently was not the soil but some small portion of it. It was therefore logical to communicate with those having similar interests. A shift of focus to the soil system would underscore the important point that soil zoologists and pedologists are working on the opposite side of the same coin. Effective soil ecology will depend upon increased cooperation between workers in these two areas.

It is true that the animal and its phylogeny or the organic-mineral complexes and their fabrics are important analytical frameworks in the respective spheres of soil biology and pedology. However, we suggest that while such perspectives facilitate analysis of parts of the soil system, exclusive commitment to these points of view has prevented synthesis. In the broader view, analysis without synthesis is a scientific dead end. Hoffman's comment that "myriapods are not just objects to be classified nor are they simply objects to produce faecal pellets" is appropriate.

Until recently, pedologists and soil zoologists have been necessarily preoccupied with description of immense natural diversity. The size of various groups of organisms, and the diversity of soils and fabrics has inevitably promoted disciplinary specialization. Unfortunately, it appears that with overemphasis on analysis, proximate goals of such specialization have become ends in themselves. We do not hold that further analytical work is either undesirable or unimportant. However, we are convinced that a general framework for synthetic work is available and that we can now proceed without waiting for more perfect descriptions of all components of the soil system. In fact, it is likely that descriptions will be improved by experimental studies of interactions among components and by information about emergent system properties that is generated through synthesis.

From information now at hand, some immediate requirements are obvious. Rusek pointed out the need to distinguish ecological groups of soil animals. This requires recognition of the reciprocity between soil animals and other soil components, and realization that soil animals are part of soil, not mere inhabitants of it. The idea is not new. In his review of the history of soil zoology, Kevan remarked that in 1757 Adamson recorded the reciprocity between termites and soil.

Real progress in science is probably often hampered by disciplinary boundaries which have been created mostly for the convenience of administrators. The willingness of scientists to adhere strictly to narrow administrative limits appears to be a recent development, even among workers interested in the soil. For example, Hoffman reported good work was done in the 19th century by people sharing their efforts among myriapods, echinoderms and mammals. A growing awareness of the reciprocity between soil animals and other soil components led to this conference and is reflected in a remark by Parkinson in his presentation: "Kubiena was remarkably perceptive both as a soil biologist and soil scientist - I suppose they are synonymous." Recognition of that unity is growing and is the central thesis of this summary and synthesis.

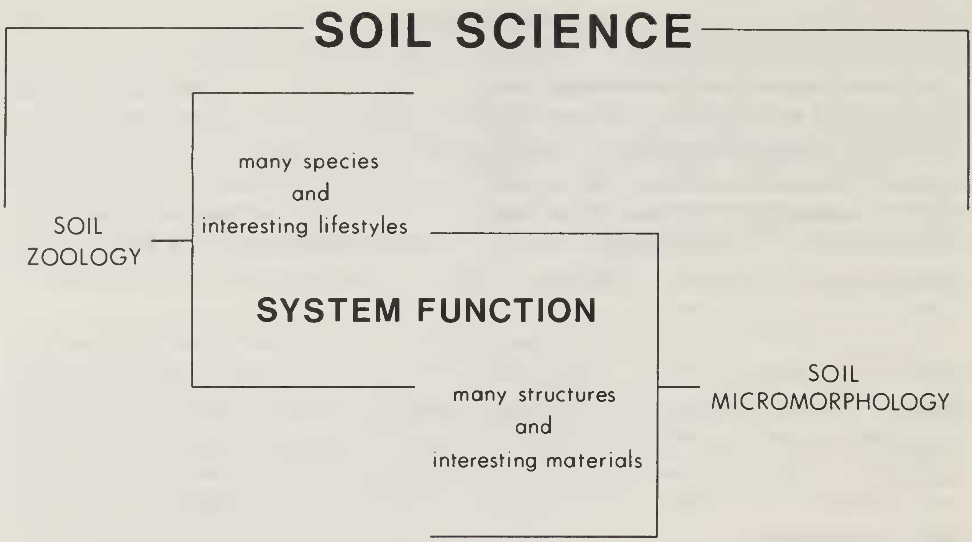

Fig. 1. Disciplinary interests showing overlap of soil micromorphology with soil zoology and the concept that the study of neither is complete without the other.

UNIFYING LINK

Systems consist of several components interacting with each other, and controlled by their environment. They are characterized by many cause-effect pathways and feedback processes, which give individuality to each system. Knowledge of that individuality is essential to structure man's interaction with ecological systems in a way that permits use of renewable natural resources that is stable in the long run. With respect to soil, it is clear that soils are being lost and degraded worldwide much faster than they are being generated and restored (Wolf, 1985).

As pointed out above, the unifying link between soil zoologists and pedologists which permits advancement of knowledge must be at a broader level of resolution than that required by either area of study alone. We argue that relationships between system function and system architecture provide that focus (Fig. 1).

For effective synthesis each part of the soil system merits detailed study and analysis in its own right. However, there are problems in each area which require information about the other. For example, while it is generally held that soil animals generate soil microstructures, it is not often clear which animals are responsible for a specific fabric or structure observed in thin sections of soil. In fact the relative impacts of soil organisms and abiotic processes are not well enough known to formulate general hypotheses. Similarly, habitable space and accessible substrates for various groups of soil animals cannot be evaluated without knowledge of soil pore size distribution and geometry relative to soil animal sizes and water film thicknesses needed to permit movement. Predator-prey interactions in soil are also controlled by pore size and geometry relative to organism sizes. Elliott *et al.* (1980) presented data consistent with the hypothesis that soil texture influences habitable pore space and hence trophic interactions in terrestrial ecosystems. The above examples show how system function and architecture unite the two disciplines. The advancement of knowledge and practical benefits mentioned earlier are to be attained at this more holistic level.

CHALLENGES

Two challenges must be dealt with before progress may be made. The first is philosophical. Kevan illustrated how past concepts of soil animals have been shrouded in mythology. Ancient bestiaries portrayed themes of morality. Also, concepts of soils have varied from the mother of all life, to masses of ground rock, depending upon perspectives of the writer (Simonson, 1968). Soils have been associated with immortality and this has been passed to animals associated with them. Hill pointed out that the above metaphysical themes can be frequently found in discussions about man's use of soils or his interactions with it (see also Hyams, 1976).

Such a theme has important cultural consequences which are amenable to investigation within classics, anthropology, and sociology. However, it may lead to two different outcomes regarding objective examination of soils and soil animals. On one hand, it may generate a set of beliefs pertaining to function of soil systems and man's interaction with them which are not amenable to scientific scrutiny because they have not been derived from objective data. It may thereby hinder objective scientific examination of biophysical and biochemical interrelations between soil animals and the structure or function of the soils of which they are a part. On the other hand, stressing that roots of agricultural man extend from the soil can lead to a determined curiosity about how the system functions and how man can appropriately interact with and even become part of it. The challenge is to assure such objective analysis and synthesis.

The second challenge is mainly taxonomic. Soil animals are among the most abundant multicelled animals anywhere on earth (up to $10^6/m^2$) and their rates of reproduction and turnover can be startling. As pointed out by many authors in this proceedings, identification and classification of soil animals is both time consuming and difficult because of their small size, great diversity and relative obscurity among other members of the animal kingdom. For example, Greenslade estimated that 130,000 species of beetles in 11 families occur in soil. As documented by Fjellberg, Hoffman and Norton, the situation with respect to other groups of important soil arthropods is equally challenging and much more poorly known. However, few workers are engaged in soil animal taxonomy and, as Hoffman lamented, there is not much support for basic taxonomic work. Because research support is society's way of establishing value and prestige of workers, few young scholars are being attracted to these vital tasks (see also Crowson, 1970). As groups of animals are made accessible through production of taxonomic monographs, links between species and their environment or interactions within the system can be better explored. Edwards' presentation dealing with the effects of earthworms on soil structure and function illustrated what sort of advances are possible through experiments once a taxon is adequately known for ecological work. However, even with respect to composition of earthworm assemblages, we are relatively uninformed in North America. Similarly, soils contain innumerable fabrics with few researchers involved in their classification.

A proposal by Greenslade may partially resolve the zoological dilemma in the short run. He suggests that taxonomists be encouraged to reverse their usual procedures and start analysis by separating large groups of important soil animals into genera and species groups. Details of species level classification can be worked out after a fauna is packaged for understanding by non-taxonomists. A first step in this important process in now underway. Dan Dindal is editing a general guide to soil zoology for North America which has been scheduled for publication by Wiley. Such treatments will be invaluable to soil biologists and should stimulate ecological work.

As noted by the Biological Survey of Canada (1982), a major impediment to development of soil ecology is a lack of taxonomic monographs and keys which are accessible to the non-specialist. Production of such material should receive high priority. As pointed out by Hoffman, the production of such basic descriptive taxonomic and faunistic work is often looked upon with disdain, even though it is most important for stimulating ecological work in the short run. Both Fjellberg and Rusek recognized need to distinguish ecological groups among taxa important in soils. Norton pointed out that study of phylogenetic relations is a major stimulus for classification and that such work has important benefits for synthetic studies. We do not argue that this approach should be abandoned. However, we submit that ecological interrelations can provide an alternative stimulus with different but complementary approaches.

Similarly, complexity of micromorphological classification of soils must be reduced and useful descriptions of microscale heterogeneity should be made available to non-specialists. The workshop session organized by McKeague and Fox provides direction for this effort. Again, synthetic work is appropriately focused by attention to the entire soil system (Fig. 2). Ultimately, this sort of work will be accomplished best by a new breed of scholar. We hope that the needs identified by this conference will be addressed by more flexible training of graduate students in soil ecology in the context of blended research programs that cross traditional departmental boundaries.

Studies of nutrient or energy flow through the soil system may be taken as an example of the above approach. Understanding energy flow requires, among other things, knowledge of where substrates are, where organisms are, and where they can go. A large proportion (40-80%) of soil pore space and surface area is inaccessible even to organisms of μm size (McGill, in preparation). Information is therefore required on physical and biological agents which reorganize soil fabrics to redistribute substrates and organisms. Such needs also link micromorphology, soil zoology and soil microbiology. The morphologist provides information on architecture, habitable spaces, and locations of substrates while soil biologists examine feeding habits and metabolism of various groups of organisms, their abilities to reorganize or produce specific fabrics, and to ingest mineral or organic material or both.

This conference has underscored the major advantages of joining the disciplines of soil zoology and pedology to foster growth of knowledge and understanding. Continued detailed analyses of each component are essential, but interactions among other components of the system can be an appropriate synthetic focus for study. We argue that the link between soil morphology and soil biology might best be described as soil biophysics. Thus, it includes but transcends faecal pellets.

SOME IDEAS

Microhabitats and Microcommunities

Although soils are viewed classically over the landscape at a macro scale of km^2 or m^2 many significant processes and mechanisms controlling them occur at a micro scale. Dindal showed that many distinct microenvironments exist in soil which lead to formation of distinct

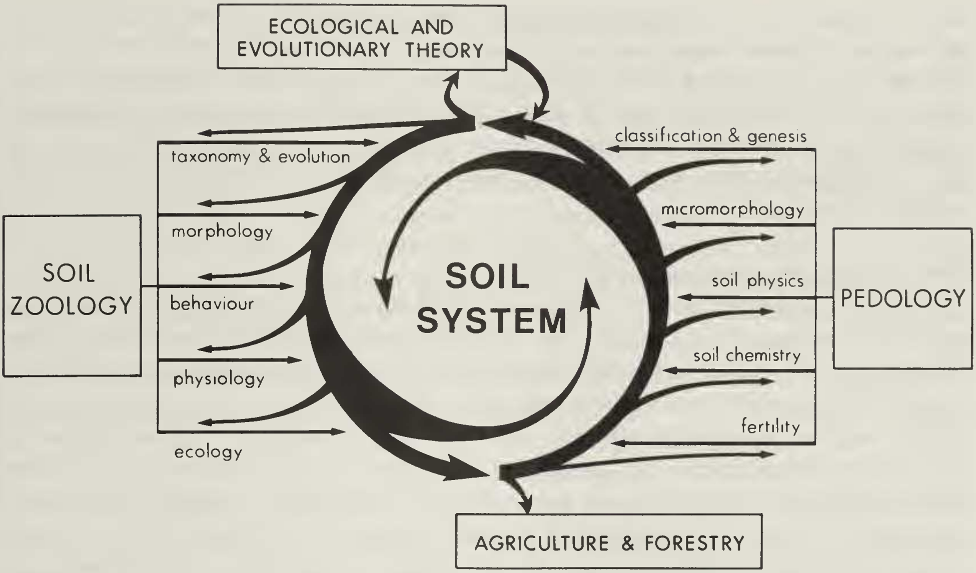

Fig. 2. Use of the soil system as a central focus for research. Work in the many subdisciplines of soil zoology and pedology can be synthesized in the dynamic framework of the soil system. The diagram emphasizes that spin-offs from synthesis will contribute to analysis in each subdiscipline. Spin-offs will also contribute to general theory and find applications in agriculture and forestry.

microcommunities and add to the spatial complexity of the macroenvironment. The soil system has tremendous spatial diversity which has been little studied in relation to its biological communities.

Implications of such microhabitat structure were cited by several authors. Greenslade estimated that only about 10,000 years are required for an area to be completely reworked by termites and Mermut showed the unique building block structures of such materials. Therefore, it is reasonable to deduce that much of the soil in tropical areas is composed of remnants of reworked termite mounds. Fjellberg mentioned that aggregation pheromones have been detected for Collembola and the resultant aggregations have obvious but unstudied implications for generation of microcommunities. Both Hill and Parkinson commented that soil animals are themselves microhabitats which move, influencing dispersal of smaller animals, bacteria and fungi. Water retained by surface tension around soil animals or their larval stages can be a significant proportion of the total water film space available to soil microorganisms (McGill, in preparation).

The guts of soil animals are also important microhabitats with respect to soil function. Parkinson mentioned that bacteria are unaffected or increase in numbers upon passage through the gut while fungi are damaged by passage through small organisms such as Collembola. The gut of earthworms is a moist microhabitat where substrates are in motion and new surfaces are acted upon by many smaller organisms. Fungal sporulation and spore movement are affected by soil pore size distribution.

A recurring theme of the conference has been the importance of faecal pellets as microhabitats which may dominate the fabric of some soils. Microcommunities and microenvironments may be characterized as mixed culture systems. Three postulates flow from this concept: (i) species interactions such as symbiosis and, perhaps, mutualism may be more characteristic and important to soil communities than are the results of succession, (ii) soil animals not only alter their own environment, but are microhabitats for smaller organisms, and (iii) the environment of a soil organism, and hence controls of its activity, are a function of its size. Investigation of these three postulates could provide an initial framework for a more synthetic soil ecology.

Fabric Reorganization and Locational Control

Pawluk emphsized that the exact involvement of soil fauna in forming soil microstructures is inadequately understood for Canadian soils. A further problem, alluded to by Mermut, is the lack of agreement among micromorphologists about standardized interpretation of soil fine structure. Because Foster and Mermut, respectively, showed that soil animals can be involved in both breakdown of structural units and in homogenization of materials, a dynamic picture of soil micromorphology emerges. It appears that soil fabrics are in a constant state of slow change; being generated, broken down and reorganized in cycles over long times. Such fabric reorganization, when combined with the above ideas about microenvironment, lead to a concept of biotic flux among substrates and environments. Such alterations in environment and relocation of organisms near fresh substrates, or in barren locations could profoundly influence how the system functions. It also provides an additional link with soil microbiology, further emphasising the mixed culture aspect of the soil system.

The role of soil fauna in comminution of plant debris and in formation of the soil matrix is becoming better understood (Seastedt, 1984). Ideas about communities developed from studies of nutrient cycling can now be extended to include disintegration or comminution of soil microstructures. Further research into this aspect of relations between soil animals and soil structure is needed before the extent and significance of the process is known. Soil microstructure influences the local environment and probability of substrate-organism contact at microsites where biological processes occur. As a result, soil organic matter dynamics, and soil quality, are influenced by fabric reorganization which comprises both formation and comminution of microstructures. Soil animals may thereby provide an important control on soil organic matter dynamics and soil quality.

Associated with the above is the effect of location, within or on soil, on the activities and survival of organisms. For example Fjelberg pointed out the sensitivity of Collembola to water supply because of the absence of an exoskeleton. One strategy is to live within soil layers where relative humidity is higher. Other soil animals migrate up and down the profile in response to soil moisture changes. Altemüller showed that what an organism does in soil is influenced by its position, and so behavioural studies of soil fauna must take micromorphological diversity into account. At an even smaller scale, Foster showed how entrapment of organic molecules or bacterial cells can result in their persistence through protection from decomposition or lysis. The above locational control on organism function is fundamental to soil systems and appears in turn to be modified by fabric reorganization. A type of feedback is thereby generated because soil animals are among the agents responsible for fabric reorganization.

SUMMARY AND CONCLUSIONS

The structure and function of soil systems are interrelated. Feedback between microhabitat conditions and soil animals is characteristic of terrestrial ecosystems. The above interactions link soil micromorphology and soil biology. System function and soil biophysics therefore become the focus which permits advancement of knowledge in soil biology and pedology beyond the capabilities of either discipline in isolation. Reciprocity between soil fauna and other soil components must be recognized, however, and studied objectively before progress can be made.

Several ideas which may help guide future research have resulted from this synthesis. It is postulated that soil fauna regulate soil systems through trophic interactions and biophysical mechanisms. Trophic interactions which involve soil animals as microhabitats have been reemphasized. Symbiosis, mutualism, and cohabitation are characteristic of soil communities, perhaps superceding in importance interactions associated with successional changes. Biophysical issues relating to size and location appear important. The relevant microenvironment of an organism is clearly a function of its size. A related concept is that the location of an organism determines its behaviour and the dynamics of its populations. We propose that comminution and disintegration of microstructures be added to formation of microstructures and comminution of plant debris as a third biophysical mechanism by which fauna regulate soil systems. Faunal influences on the dynamic relationships between soil structure and function should receive major emphasis.

An immediate challenge remains to link specific groups of soil organisms to defined soil microstructures as seen in thin sections. Related to this challenge is our recommendation for a more ecologically useful approach to classifying both organisms and soil fabrics which is needed to permit such links to be developed.

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ADDENDA: TECHNIQUES, EQUIPMENT, ADDITIONAL REFERENCES, AND PRIORITIES FOR FUTURE STUDY